Finding optimal stimuli ensemble of a cortical network

Noelia Montejo, Jean-Luc Blanc, Laurent Pezard

APPLICATION OF BLAHUT-ARIMOTO ALGORITHM: FINDING OPTIMAL STIMULI ENSEMBLE OF A NEURAL NETWORK.

Noelia Montejo, Jean-Luc Blanc and Laurent Pezard
Laboratoire de Neurosciences Intégratives et Adaptatives
UMR 6149 - CNRS - Aix-Marseille Université

ABSTRACT
We explore the determination of the optimal stimuli ensemble of a cortical network on the basis of numerical simulations of a local recurrent network. The optimal stimulus ensemble is determined with the Blahut-Arimoto algorithm using indices of population activity (multiunit activity and local field potentials). We show that the optimal stimulus ensemble is characterized by a distribution where the stimulus which induces a change in the dynamics of the network is highly represented. These results suggests that bifurcation points in the networks dynamic are highly informative and we are in accordance with preliminary observation of electrophysiological recordings.

KEYWORDS
Spike trains, Information theory, neural network, BRIAN simulator.

1 Introduction

The nature of the neuronal population coding remains one of the fundamental problems in the neurosciences. Several alternatives have been proposed e.g. information could be carried in spike rate, spike timing, local field potential (LFP), spike correlations within single neurons, spike correlations across neurons, or any combination of these. Nevertheless, to decide between these alternatives, it is necessary to know what specific stimulus features are encoded. For example: do spike counts encode the amplitude or the frequency of a sinusoidal stimulus. A widely used approach to neural coding is to treat the brain as a communication channel and compare the information about stimuli available in different candidate codes in an information theory framework [5, 12]. Information theory introduces mutual information which gives a comprehensive quantification of the information contained in a neuronal population, by evaluating the reduction of uncertainty about the stimuli that can be obtained from the neuronal responses.
Accurate estimation the information that spike trains convey about external stimuli is fraught with a major practical difficulty: information theoretic measures suffer from a significant systematic error due to the limited amount of stimulus-response data that can be realistically collected in an experimental session [13]. However, the advantages of a single-trial population analysis over traditional single-cell studies of trial averaged responses, have been described in [6], in particular, how information that is ambiguous at the single-cell level can be clearly interpreted when considering the whole population.
Input-output systems are investigated by using either a predefined set of inputs or inputs drawn at random from a predefined probability distribution. However, both approaches risk missing important regions in input space. If interest concerns the system's function in terms of information transmission, then the data acquisition can be significantly improved by using an iterative algorithm [4] which orients the search in the input space. The optimal input ensemble itself might be interpreted as representing the region in input space that a particular system preferentially encodes.
In this paper, our system is an excitatory-inhibitory recurrent network model where the strength of the population oscillation strongly depends on external inputs to network and synaptic connections.
Our network is composed of simple of integrate-and-fire neurons [10] with a determined synaptic kinetics. This choice of model network permits us code the neural activity through the firing rate of a single cell and/or the whole network and the local field potential (LFP).
The aim of the present study is to show how the interaction between stimulus oscillations and neural oscillations allow the population activity to transmit information about the signals received by the network and to find the optimal stimuli ensemble.

2 Model of cortical network

We used a model of cortical network composed of $N = 5000$ leaky integrate-and-fire neurons. This model network represents a simplified local recurrent circuit in primary sensory cortex and is composed of 20% of inhibitory interneurons and 80% of excitatory pyramidal neurons [2]. The connections between any directed pair of cells are random with a probability of connections equals to 0.2.
The description of each cell (pyramidal and interneuron) is describe in [2] Eq. 1, with the values of parameters shown in Table 1
We considered that excitatory post-synaptic currents (EPSC) originating from a presynaptic pyramidal cell consist of I_{AMPA} and the inhibitory post-synaptic currents (IPSC) originating from an interneuron is assumed to be mediated by GABA-A receptors. Both AMPA and GABA-A receptors mediated currents $I_{AMPA} = g_{AMPA}s(V_m -$

	Pyramidal cell	Interneuron
$\tau_m = C_m/g_L$	20 ms	10 ms
C_m	0.5 nF	0.2 nF
g_L	0.025 μS	0.02 μS
V_{th}	-52 mV	-52 mV
V_{reset}	-59 mV	-60 mV
V_L	-70 mV	-65 mV

Table 1: Parameters of excitatory and inhibitory neurons.

V_E) with $V_E = 0mV$ and $I_{GABA} = g_{GABA}s(V_m - V_I)$ with $V_I = -70mV$, respectively. The gating variable s (fraction of open channels) is described by two first-order kinetics, [3]:

$$\begin{aligned} \frac{dx}{dt} &= \phi(\alpha_x \sum_j \delta(t - t_j) - x/\tau_r) \\ \frac{ds}{dt} &= \phi(\alpha_s x(1 - s) - s/\tau_d) \end{aligned} \tag{1}$$

where the sum is over presynaptic spike times. The scaling factor ϕ controls the speed of synaptic kinetics without affecting the steady state. The strength of GABAergic connections was sufficient to ensure stable activity at low firing rates in the network.

	Pyramidal cell	Interneuron
τ_r^{AMPA}	0.4 ms	0.2 ms
τ_d^{AMPA}	0.20 ms	1.0 ms
τ_r^{GABA}	0.25 ms	0.5 ms
τ_d^{GABA}	5.0	5.0 ms
g_{AMPA}	0.19 nS	0.3 nS
g_{GABA}	2.5 nS	2.25 nS

Table 2: Parameters of excitatory and inhibitory synapses.

Both populations received a noisy excitatory external input taken to represent the activity from thalamocortical afferents, with interneurons receiving stronger inputs than pyramidal neurons. These excitatory afferents are represented by a Gaussian white noise with mean $\mu = 0.3$ nA and variance $\sigma^2 = 0.018$ nA. The external input were assumed to arise from 800 external synapses of AMPA type, with conductance 0.25 nS (on pyramids), 0.4 nS (on interneurons), and the same kinetics as recurrent AMPA synapses. These synapses are activated by random Poisson spike trains, with a time-varying rate, given by

$$\nu_{signal}(t) = Asin(2\pi\omega t) \tag{2}$$

The activity of the network is quantified by monitoring the individual spike times of each neuron, the instantaneous population firing rate (obtained counting the number of spikes fired by neurons in a given population in a 1 ms bin), the average membrane potential of each population, and the average synaptic currents. In order to compare the oscillations of the model to those recorded in cortex, the LFP (local field potential) is computed from the network as the sum of the absolute values of AMPA and GABA currents $\langle |I_A| + |I_G| \rangle$ on pyramidal cells [2].

3 Information theory framework

Mutual information I quantifies how much information the neural responses convey about a sensory stimuli set. Let's consider a time window T associated with a sensory stimulus s chosen with a probability $p(s)$ from a stimulus set $S = \{s_1, s_2, ..., s_m\}$ during which the activity of N neurons is recorded. The neuronal population response is denoted by the random variable $R = \{r_1, r_2, ..., r_n\}$, where r_i is the response of neural population within the time window T. In a spike count code, the response is the number of spikes within the time window T. In a spike timing code, the response is a sequence of spike firing times.
The conditional probability distribution $p(r|s)$ describes how the system relates inputs to outputs. The amount of information I (difference between the Shannon entropy of responses $H(R)$ and the noise entropy $H(R|S)$) that is conveyed by such a system depends on both $p(r|s)$ and the prior distribution of input $p(s)$:

$$I(R;S) = H(R) - H(R|S) \tag{3}$$

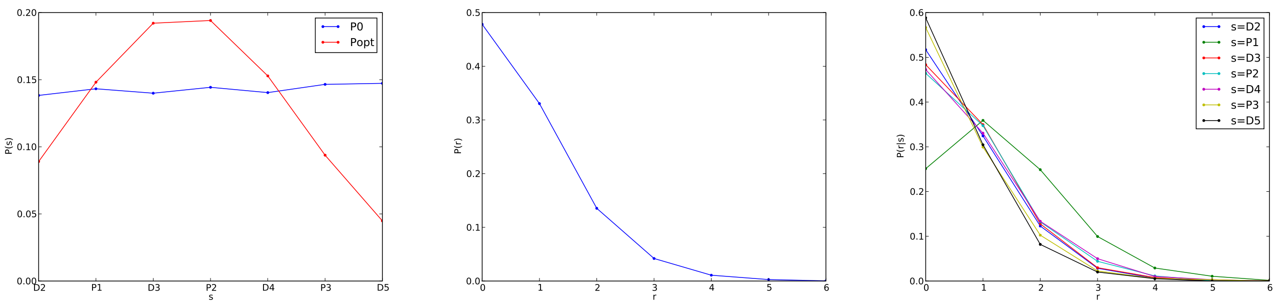
$$I(R;S) = \sum_s p(s) \sum_r p(r|s) log_2 \frac{p(r|s)}{q(r)} \tag{4}$$

where $q(r) = \sum_s p(r|s).p(s)$ is the marginal probability associated to the neural response r.
Channel capacity C is a fundamental concept, introduced by Shannon [18] in information theory, which specifies the limit on the maximum rate at which information can be conveyed reliably over a channel:

$$C = max_{p(s)} I(R;S). \tag{5}$$

The mutual information is bounded by the channel capacity of the system, where the maximum is determined with respect to all possible input distributions $p(s)$. In our context, the specific stimuli distribution $p^*(s)$ that reaches this information capacity corresponds to an optimal stimulus ensemble and is denoted $p_{opt}(s)$.
Evaluation of channel capacity C is a standard maximization problem of a convex function which can be solved using the method of Lagrange multipliers and gives the optimum input distribution in an iterative way, this algorithm was established by Blahut and Arimoto [16, 17]. Given a conditional response distribution $p(r|s)$, the algorithm allows to determine an optimal stimulus ensemble $p_{opt}(s)$. At first step $n = 1$, we construct an initial stimulus ensemble $p_n(s) > 0$, for example a uniform distribution. Then, we iterate the equation:

$$\begin{aligned} p_{n+1}(s) &= ZP_n(s) e^{\sum_r p_n(r|s) log_2 (\frac{p_n(r|s)}{q_n(r)})} \\ q_n(r) &= \sum_s p_n(r|s) p_n(s) \end{aligned} \tag{6}$$



(a) Probability of stimuli : p(s) (b) Probability of response : p(r) (c) Conditional response Probability : p(r/s)

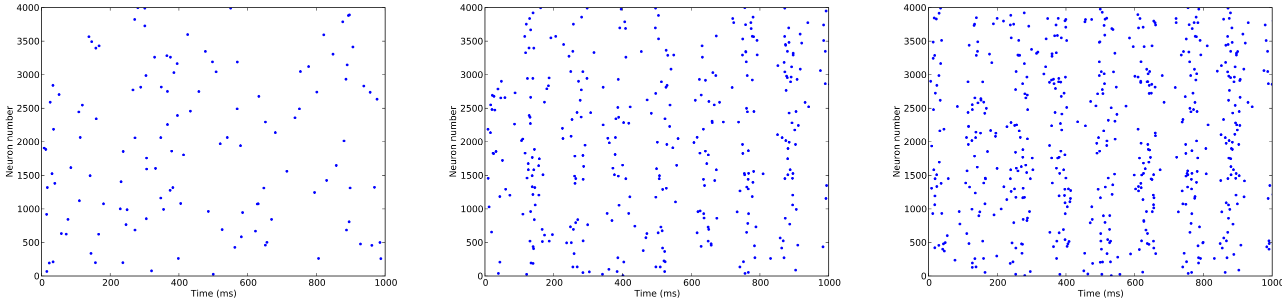
Figure 1: Example of Blahut-Arimoto algorithm application: off-line evaluation on experimental data from somatosensorial cortex of rat. Data corresponds to a single unit obtained from multi-unit activity with spike sorting. The set of initial stimuli are $s = \{D2, P1, D3, P2, D4, P3, D5\}$ with a homogeneous probability $p(s) \approx 0.15$, that is represented by blue line in (a). The stimuli are tactile and are applied in four of digits: D2, D3, D4, D5 and three localizations of paw: P1, P2, P3, [9]. The set of response (spike count) $r = \{0, 1, 2, 3, 4, 5, 6\}$ with a probability shown in (b). the conditional probability is plotted in (c). We used the algorithm, Eq. 6, in order to find the optimal stimuli, red line in (a).

where Z is a normalization function determined at each iteration $Z = \frac{1}{\sum_s p_{n+1}(s)}$. The exponent term corresponds to the Kullback-Leibler distance between $p_n(r|s)$ and $q_n(r)$ and will diverge if the two distributions strongly differ. As a result, the Blahut-Arimoto algorithm increases the probability $p(s)$ of an informative stimulus s and decreases the probability $p(s)$ of an uninformative stimulus s whose conditional response distribution $p(r|s)$ is similar to $q_n(r)$. For $n \to \infty$, the algorithm converges to an optimal stimulus ensemble, $p_n(s) \to p_{opt}(s)$.
As example of application of Blahut-Arimoto algorithm on physiological data from somatosensorial (S1) cortex, obtained from [9], the Fig 1 shows the procedure of algorithm on a single cell. This evaluation is off-line, that means, the data is from [9], then a spike sorting is carried out in order to look for single units and calculated their receptor fields. We chose a single neuron, from nine obtained, with a receptor field in $s = P1$. In Fig 1 (a) the initial probability of stimuli is plotted: blue line. In Fig. 1 (b-c) we plot the necessary probabilities of Eq. 6, $p(r)$ and $p(r|s)$, in this example for a our single unit, this values are replaced in the iterative Eq. 6. In Fig 1 (a) , we found out the optimal stimuli for this neuron that is represented for red line in Fig. 1 (a), where we can see the stimuli are different from the receptor field. That is, the neuron conveys more information quantity for stimuli $s = D3, P2$ than for its receptor field.

4 Simulations results

We used the BRIAN simulator [15] to simulate the cortical network in order to apply the Blahut-Arimoto algorithm. In this paper, we only present results of spike count and not of measures of LFP.
The Fig.2 describes the dynamics of network for three different stimulus, where each stimulus is a poissonian spike train whose rates are Fig.2(a) $A = 2400$, (b) $A = 5000$ Hz and (c) $A = 8000$ Hz. The figure shows the raster plots for each stimulus, where we can observe that the synchronization occurs when there is a balance between excitation and inhibition synapses and the external input (that is a represented by excitatory synapses coming from the thalamus), that means when the parameter $A > 3000$ Hz, where clusters of synchronization begins to appear. Every stimulus has two control parameters: amplitude of signal A and the modulated frequency ω, Eq.2. The Fig 3 shows the tunning curve. In this figure we can observe that dynamic of the network is controlled by the amplitude of signal A and not by ω, figure not shown.

The optimization algorithm of Blahut-Arimoto [4, 7] is applied to network model of [2] Eq. 1, where the duration of stimulus is 500 ms and it is applied after 500 ms of begin of simulation. We did 1000 trials, each stimulus is repeated 100 times in random way. A list of spike count for every stimulus is saved. With this list of response, we used the optimization algorithm. During the iterative procedure each step corresponds to the presentation of a specific stimuli distribution p and for this collection of stimuli the neural network gives a set of neural responses with a probability distribution q. We can obtain an optimal stimuli ensemble S_{opt}, when the stimuli distribution p_{opt} generates neural responses with a distribution q where the distance between this two probability distributions $D(P||Q)$ is minimal, i.e. when the mutual information between the stimuli random variable S_{opt} and the neural responses R is maximal. Fig 4 shows the optimal distribution obtained by Blahut-Arimoto algorithm, Eq. 6, the initial distribution is homogeneous with $s_i, i = 1, ..., 10$, there are ten stimuli and every one is repeated one hundred times. In Fig.4 initial (homogeneous) and optimal distribution are plotted in black and red curves respectively. In this plot the response analyzed is the spike rate of network.



(a) $A = 2400$ Hz (b) $A = 5000$ Hz. (c) $A = 8000$ Hz.

Figure 2: Dynamics of network receiving three different stimuli $\omega = 8$ Hz. The parameter A is described in the Eq.2.

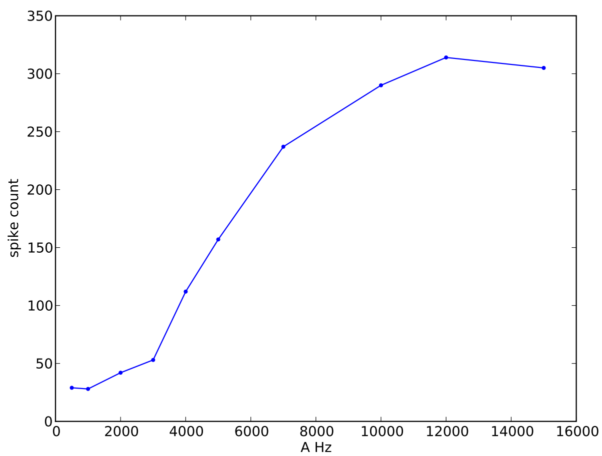


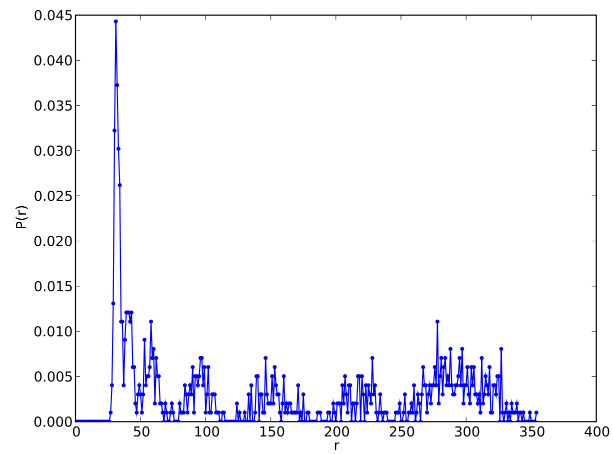
Figure 3: Tunning curve of network for parameter A of stimulus with $\omega = 8$ Hz.

5 Conclusion

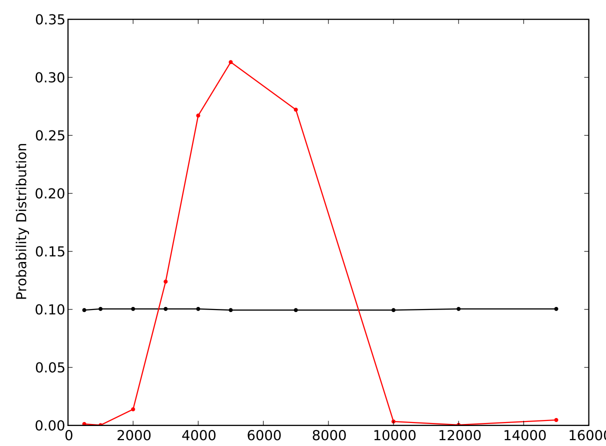
We can observe that the optimal stimulus corresponds to the stimulus where the network dynamic changes slowly. Considering the tunning curve, this optimal stimulus is in the range of stimulus where the response begins to change and where clusters (synchronized neuron's groups) begin to appear.

The Blahut-Arimoto algorithm has been tested in a single neuron model [4] and *in vivo* [7]. We applied this algorithm in a neural network model, but the proposed method could therefore serve to find the ensemble of stimuli that a given neural system naturally expects.

In order to investigate if, and in which way, a given sensory system is optimized with respect to its environment, we propose to test this procedure like a systematic online search for the ensemble of stimuli that are encoded best, using the live responses of receptor neurons as a guide. The attributes of the determined optimal stimulus ensemble can then be compared to the stimuli of the organism's natural environment [6].



(a) Probability of response: $P(r)$



(b) Probability of stimuli: $P(s)$

Figure 4: Application of Blahut-Arimoto algorithm on a neural network. (a) The different responses with their probability. (b) The initial (black curve) and optimal (red curve) probability distribution of stimuli.

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